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Optimal energy allocation to ovaries after spawning

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ABSTRACT

For iteroparous organisms in which fecundity is positively related to body size, a trade-off exists between allocation of energy to gonads, thus ensuring some reproductive output, and allocation to somatic growth, thus increasing potential fecundity in the future. This tradeoff can influence several life-history patterns, including when, for organisms that grow after maturity, allocation to gonads begins following the previous reproductive event. White crappie *Pomoxis annularis*, a spring-spawning freshwater fish, began allocating energy to ovaries in autumn at the expense of continued somatic growth and higher potential fecundity. Within five populations, the amount of early allocation varied between years. We combined dynamic programming with an individual-based model to determine how summer and spring feeding conditions interact to influence when allocation to reproduction should begin. Model results indicated that autumn allocation to ovaries was in response to future spring feeding conditions rather than recent summer feeding conditions. At least a 10% probability of poor spring feeding conditions resulted in ovary investment patterns that matched field observations. The model was unable to explain the inter-annual variation in autumn energy observed in the field. Early allocation of energy to ovaries is probably an evolutionary adaptation to the possibility of poor spring feeding conditions.

INTRODUCTION

When energy resources are limited, how an organism partitions energy between somatic (storage or growth) and reproductive tissues will influence its lifetime fitness (Fisher, 1930). For iteroparous organisms, optimal energy allocation will be a response to the trade-off between current reproductive development and somatic growth towards future reproductive development (Williams, 1966). This trade-off is most pronounced in organisms for which body size is positively related to fecundity because energy allocated to somatic rather than reproductive growth can enhance future potential fecundity. Over the reproductive life of an organism, this trade-off can influence several life-history patterns, including age at first reproduction, whether an organism allocates energy to somatic growth after reproduction and when, in organisms that grow after maturity, allocation to reproduction begins after the previous reproductive event. Variability in food (Gurney and Middleton, 1996; Shertzer and Ellner, 2002) or length of growing season (Hom, 1987; Kozlowski and Teriokhin, 1999) as well as mortality (Kozlowski and Uchmanski, 1987; Pugliese, 1987; Pugliese and Kozlowski, 1990; Engen and Saether, 1994; Heino and Kaitala, 1996; Kozlowski and Teriokhin, 1999) are predicted to influence both age at first reproduction and growth after maturity. For organisms that grow after maturity, we suggest that similar factors may influence when allocation to gonads should begin following a reproductive event.

Our modelling efforts centred on energy allocation between reproductive events for organisms that grow after maturity and whose body size and fecundity are positively related. We used the model to determine how soon allocation to reproduction should begin, given the costs to

potential fecundity. Consider two contrasting strategies. An 'early' strategy allocates energy to somatic growth for a relatively short period before beginning energy allocation to gonads. This strategy maximizes the chance that an individual has developed gonads by the next reproductive opportunity, but compromises somatic body size, limiting potential fecundity for the next reproductive event. Alternatively, a 'late' strategy increases body size and maximizes potential fecundity by allocating energy to somatic growth for a relatively long period, before beginning energy allocation to gonads. In this case, however, the organism risks not having sufficient time or energy to maximize gonad size before the reproductive opportunity arises.

Iteroparous fish provide an excellent model to explore this trade-off as they generally grow after maturity. In addition, after a summer of growth, many temperate freshwater fish species begin allocation to reproduction (i.e. ovaries) during autumn, 6 months before reproduction in the following spring (largemouth bass *Micropterus salmoides*: Adams *et al.*, 1982a; walleye *Stizostedion vitreum*: Henderson and Nepszy, 1994; yellow perch *Perca flavescens*: Henderson *et al.*, 2000). In the present study, we provide field data showing that five populations of white crappie *Pomoxis annularis* began allocating energy to ovaries as soon as autumn, despite not reproducing until the following spring. Within populations, the amount of energy allocation varied between years.

We used a dynamic programming model to determine why allocation of energy to reproduction, rather than somatic growth, might be optimal during autumn and why white crappies would allocate more in some years than others. We thought this 'early' allocation to ovaries could be in response to either one or both of the following: a plastic response to recent good feeding conditions during summer or an evolutionary response to poor feeding conditions during the coming reproductive season. Although either of these may explain the general occurrence of early allocation to ovaries, only the first of these (i.e. a plastic response to recent feeding conditions) can explain year-to-year differences in the amount of allocation to ovaries.

Dynamic programming is perfectly equipped to explore these two scenarios simultaneously, as it can provide state (e.g. length, ovary size, current feeding conditions) dependent energy allocation decisions (where state dependence can be thought of as a response to past conditions) that optimize lifetime reproductive fitness in a framework that considers expected future fitness (which can be thought of as an expression of 'evolutionary experience'). In the dynamic programming model, optimal allocation decisions were made by fish exposed to different summer and spring feeding conditions. To allow us to compare allocation decisions arising from the optimality model with data collected from white crappie in Ohio reservoirs, we embedded the output from the dynamic programming model within an individual-based simulation model. Growth and gonadal investments of the simulated cohort of 'optimal' fish were then compared to those of populations of Ohio fish to determine whether summer or spring feeding conditions influence energy allocation decisions of white crappie in Ohio reservoirs.

METHODS

White crappie life history

White crappies are native to lakes and low-gradient rivers east of the Rocky Mountains (Trautman, 1957), but have been introduced as far west as California (Goodson, 1966) because of their popularity as a sportfish. White crappie growth is generally fastest during early summer (Gabelhouse, 1991; Guy and Willis, 1995), when prey are abundant and water temperatures are increasing. In Ohio, white crappies typically mature by 2 years of age, although slow growth may delay maturity (Bunnell *et al,* 2000). Reproduction begins when water temperatures rise to

near 14°C in the late spring or early summer (Siefert, 1968) and typically lasts 6-8 weeks, which generally is early May to mid-June in Ohio (Bunnell *et al.*, 2000).

Field sampling

During 1998, conspicuous ovaries were observed in a few white crappies that were sacrificed for age estimates during an autumn population sample in two reservoirs. In 1999–2000, however, ovaries of all sizes of sacrificed fishes were removed from an additional three populations to document more systematically autumn ovary investment. In these years, ovaries were measured (to the nearest 0.1 g) in up to six fish per centimetre size class (range = 1–6 fish and median = 2 fish) in each reservoir. In all years, adult white crappies were captured in trapnets (Colvin and Vasey, 1986). Upon capture, the fish to be sacrificed were placed on ice and then returned to the laboratory. Their sex was determined, they were weighed to the nearest gram and measured to the nearest millimetre. The gonadosomatic index [GSI = (ovary mass (g)/total body mass (g)) × 100%] was estimated for all females.

To determine whether ovarian investment of individuals differed across reservoirs or years in which different sizes of white crappie were sampled, we first calculated ovary mass residuals from the linear relationship between autumn ovary mass and total mass. We then used a general linear model (PROC GLM; SAS Institute, 1999) with residual ovary mass as the dependent variable and reservoir, year and the reservoir × year interaction as explanatory class variables.

Modelling overview

We used dynamic programming to identify optimal energy allocation decisions under a variety of summer and spring feeding conditions. First, the model determined state-dependent optimal allocation to somatic growth (length) or ovaries when feeding conditions were constant across years. Next, it determined optimal allocation when spring feeding conditions randomly varied between years. These state-dependent and feeding environment-dependent (both amount and certainty of food) optimal allocation decisions were then used by simulated fish in an individual-based model. This allowed us to translate optimal energy allocation decisions into seasonal growth dynamics of somatic and reproductive tissues, which, in turn, could be compared with the seasonal growth of somatic and reproductive tissue of white crappie from Ohio reservoirs.

Dynamic programming model

The objective of this model was to determine how fish length (L, in centimetres), ovary size (G, in grams) and quality of feeding conditions (P) influence optimal allocation of energy to somatic growth (κ) during each season (t) for female white crappie. At the end of each season, L' and G' are the new lengths and ovary masses arising from optimal allocation. A general growth efficiency function for poikilotherms was used to estimate somatic and ovarian growth (i.e. change in mass, ΔM, in grams) as a function of consumption, I (in grams):

$$\frac{\Delta M}{I} = cM^{h} \qquad (1)$$

where c = 0.21 and h = -0.05 (Peters, 1983). Given that $M' = M + \Delta M$, we substituted into equation (1) and solved for M':

$$M' = M + IcM^h \quad (2)$$

Because our model monitors length (L) rather than body mass (M) of fish, we use $M = aL^b$ to transform M' in equation (2) to L'. Thus,

$$L' = \left(\frac{aL^b + \kappa Ic(aL^b)^h}{a}\right)^{1/b} \quad (3)$$

where $a = 4.90 \times 10^{-3}$ and $b = 3.332$ (Bunnell *et al.,* 2000) and κ is the decision variable that represents the proportion of available energy allocated to somatic growth.

Gonad mass at the end of each growing season, G', had the same basic structure as equation (2), except that we assumed ovaries required more energy to grow. Ovarian tissue is approximately 1.33 times the energy density of somatic tissue (D.B. Bunnell, unpublished data). Thus

$$G' = G + j(1-\kappa)Ic(aL^b)^h \quad (4)$$

where $j = 0.75$ to account for the high energy density of ovaries and $(1 - \kappa)$ represents the proportion of energy allocated to ovarian growth. Because ovary size is constrained by fish size, we used the relationship between white crappie length and ovary mass in Ohio reservoirs (Fig. 1a) to set the maximum ovary size:

$$G_{max} = 2.252^{-8}(L)^{6.0926} \quad (5)$$

In each season, consumption, I, was modified with the variable P, which represents quality of feeding conditions in a particular season. Ranging from 0 to 1, P also can be considered the proportion of maximum consumption, where maximum consumption (I_{max}) is a function of both season (t) and fish length (L):

$$I = PI^{max}(t, L) \quad (6)$$

Seasons were defined as summer (June–August), autumn (September–November), winter (December–February) and spring (March–May). To estimate average seasonal temperatures in Ohio, we calculated mean seasonal water temperatures of 10 Ohio reservoirs of varying latitude (Table 1). We then used the temperature-dependence function from the white crappie bioenergetics model (Hayward and Arnold, 1996; Zweifel, 2000) to determine I_{max} (g prey·g^{-1}·day^{-1}) for each season: summer was 3.8% of body mass per day, autumn was 1.46% of body mass per day, winter was 0.26% of body mass per day and spring was 0.82% of body mass per day.

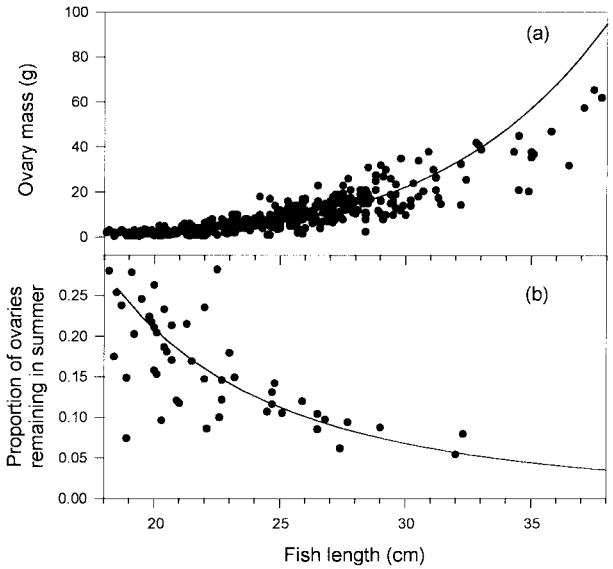

Fig. 1. Statistical functions used to describe ovary size in the models, derived from field data (Bunnell *et al.*, 2000) collected from Ohio reservoirs. (a) Maximum ovary mass (g) as a function of fish length (cm) (equation 5). (b) Proportion of ovaries remaining after spring spawning as a function of fish length (cm).

For each season t, a modelled fish chose the allocation strategy that maximized expected fitness from t to terminal time (T), given its current states L, G and P. We made $t = 1$ correspond to summer for a fish of age 2 years. We assumed spawning occurred at the end of spring; thus, ovary size at the end of spring, immediately before spawning, was the maximum ovary size attained. After spawning in the beginning of summer, ovary mass was reduced as a function of L as $843.7/L^{2.7696}$ (Fig. 1b), which was estimated from field sampling of adult female white crappie during April through August in one Ohio reservoir (Bunnell *et al.*, 2000).

Fitness was measured in terms of expected number of larvae produced. Number of larvae produced in a given year was a function of ovary mass at the end of spring. We assumed that there were 10,000 mature ova per gram of ovary (Bunnell *et al.*, 2000) and that 10% of fertilized eggs hatched successfully:

$$\text{larvae}(G)=10{,}000\times(0.1)G \qquad (7)$$

Modelled individuals chose the proportion (κ) of available energy to allocate to somatic growth such that expected lifetime larval production was maximized. We used backward iteration

Table 1. Summary of seasonal water temperatures in 10 Ohio reservoirs during at least 2 years (mean ± standard deviation)

Season	Months	n	Temperature (°C)
Summer	June–August	12	24.0 ± 2.0
Autumn	September–November	3	15.1 ± 5.8
Winter	December–February	4	4.1 ± 1.7
Spring	March–May	5	11.1 ± 5.5

(Mangel and Clark, 1988) to find the optimal solution. In a non-spawning season (i.e. summer, autumn, winter), we calculated $F(L, G, P, t)$, the maximum expected future fitness from t to T for a fish of length L, with ovaries of mass G, experiencing feeding conditions of quality P during season t, that could experience one of two different feeding conditions, P_1 and P_2, during the next season $t + 1$, with probabilities ρ_1 and ρ_2, as:

$$F(L, G, P, t) = \beta \max_{0 \le \kappa \le 1} [(\rho_1 F(L', G', P_1, t+1) + (\rho_2 F(L', G', P_2, t+1)] \qquad (8)$$

where β is the probability of surviving the current season. In a spawning season t (i.e. spring), maximum expected future fitness is

$$F(L, G, P, t) = \beta[\max_{0 \le \kappa \le 1} [(\rho_1 F(L', G', P_1, t+1) + (\rho_2 F(L', G', P_2, t+1)] + \text{larvae}(G')] \qquad (9)$$

Because T corresponds to a summer time-step, $F(L, G, P, T) = 0$.

Seasonal survival, β, equalled 0.86, which corresponds to an annual probability of survival of 0.55, falling within the range (0.37–0.88) of annual survival estimates of white crappie in Ohio reservoirs (D.B. Bunnell, unpublished data). Because lifespan varies between fish and to avoid the effects of an artificially constant lifespan, our model simulated uncertain terminal time for fish by setting T to 49. We have no reason to believe that seasonal survival rate changes with age. Under this assumption, the probability of a fish surviving from time $t = 1$ to $t = T$ is 0.0007. Because white crappie rarely live to age 6 years, we used output only from $t = 1$ to 16 (corresponding to summer for a 2-year-old fish through spring for a 5-year-old fish), although optimal solutions took into account the possibility of these fish living beyond age 5. The range of lengths of fish evaluated in the model was 11.5–44.5 cm. Although fish less than 18.5 cm could have small (< 0.5 g) ovaries, we never observed 2-year-old white crappie less than 18.5 cm to have conspicuous ovaries during field sampling. Thus, we set $\kappa = 1$ (i.e. allocate all energy to somatic growth) for all fish less than 18.5 cm.

Effect of constant summer and spring feeding conditions across years

The variable for feeding conditions, P, was used to vary summer and spring consumption. To determine how summer and spring feeding conditions influence optimal energy allocation, we completed a 2 × 10 factorial design of model runs in which one of two summer feeding conditions and one of ten spring feeding conditions occurred each year. Because seasonal feeding conditions did not change between years, the probability (ρ_1) of the first feeding condition (P_1) occurring was 1.0 and the probability (ρ_2) of the second feeding condition (P_2) occurring was 0.0 in all treatments. Summer feeding conditions were either poor ($P_1 = 0.2$) or good ($P_1 = 0.6$) in a set of simulations, whereas spring feeding conditions took a value from 0.1 to 1.0 at intervals of 0.1 in a set of simulations. In all treatments, autumn and winter feeding conditions were always the same (i.e. $P_1 = 0.4$, $\rho_1 = 1.0$).

Effect of variable spring feeding conditions across years

To determine how randomly varying spring feeding conditions influenced optimal energy allocation, we completed a 2 × 9 factorial design of model runs in which one of two summer feeding conditions occurred each year and one of nine different probabilities of poor spring feeding conditions occurred each year. The summer feeding conditions were the same as in the

previous factorial design. In a given spring, however, spring feeding conditions were either poor (P_1 = 0.2), with probability p_1, or good (P_2 = 0.6), with probability ρ_2 = 1 — P_1. The probabilities of poor spring feeding conditions were 0.0, 0.01, 0.05, 0.1, 0.2, 0.4, 0.6, 0.8 and 1.0. Again, in all treatments, autumn and winter feeding conditions were the same each year (i.e. P_1 = 0.4, ρ_1= 1.0).

Individual-based model

In this model, we used the optimal state- and time-dependent energy allocation decisions (κ) from the dynamic programming model output to determine seasonal growth (somatic and ovary) for individuals in a cohort of white crappie. We ran the same two factorial designs of summer and spring feeding conditions as in the dynamic programming. At the initiation of each model run (t=1, corresponding to summer), 1000 fish were drawn from a normal distribution of lengths (mean =19.3 cm, standard deviation = 1.6), which represents a typical length distribution of 2-year-old white crappie in the summer in Ohio (D.B. Bunnell, unpublished data). We assumed that white crappie reached maximum ovary size by the end of spring and then spawned at the beginning of summer. Thus, in the first season of the simulation, pre-spawning ovary size was drawn from a normal distribution (mean = length-specific G_{max} from equation 5; standard deviation = 0.5), which was then immediately reduced, due to spawning, by the same fraction as in the dynamic programming model. For each of the 16 seasons (time-steps), fish growth (i.e. equations 3 and 4), constraint of ovary size (equation 5) and probability of survival, β, all were equal to that of the dynamic programming model. Similarly, seasonal consumption (equation 6) was determined by season, fish length and feeding conditions. The probability of a specific feeding condition P_i was again set by ρ_i. We monitored the somatic growth and ovarian investments of these modelled fish. Because field data on ovary mass are often expressed as the gonadosomatic index (GSI), we expressed our simulation results in this form. Within each treatment, we first calculated the mean GSI for each millimetre length class of fish of a given age in a given season, across the 10 simulations. Across each centimetre length class, we then calculated a grand mean GSI. We then calculated a final grand mean GSI across all fish lengths.

As a check on whether the model was generating reasonable results, we used the individual-based model to generate growth trajectories and pre-spawning GSI of modelled white crappies. For each of six different feeding treatments, which ranged from the worst to the best possible feeding conditions, we calculated the mean length at age in each season and mean GSI at the end of spring for each simulation and then a grand mean across simulations. We then compared mean length at age and pre-spawning GSI of modelled fish to those sampled in Ohio reservoirs.

RESULTS

Field results

During autumn, we collected ovaries from 238 white crappies across two reservoirs in 1998, four reservoirs in 1999 and five reservoirs in 2000. Conspicuous yellow ovaries were observed in all white crappie, but autumn GSI varied between reservoir-years (Fig. 2). Across reservoir-years, mean autumn GSI ranged from 1.0 to 3.1, and the GSI of fish in Alum Creek in 1998 was noticeably higher than that of all others. The mean autumn GSI of all fish collected was 1.4. In late April, about 2 weeks before spawning, a white crappie 25 cm in length (about the average fish size sampled in autumn) has an average GSI of 4.0 (D.B. Bunnell, unpublished data). Thus, by autumn, the average fish had developed at least 30% of its ovary mass for the

following spring.

Residual ovary mass (residuals from the linear relationship between ovary mass and body mass) was used to determine whether ovary size - a measure of energy allocation available from fishes sampled in the field - differed between years or reservoirs. Residual ovary mass was influenced by reservoir ($F_{4,226}$ = 13.70, $p < 0.0001$), year ($F_{2,226}$ = 45.13, $p < 0.0001$) and the reservoir × year interaction ($F_{5,226}$ = 23.88, $p < 0.0001$). Because we were interested in whether the large ovaries measured in Alum Creek in 1998 drove these results, we removed all Alum Creek observations from the data set and repeated the analysis. The reservoir × year interaction remained significant ($F_{3,190}$ = 11.62, $p < 0.0001$), but the p-values associated with reservoir ($F_{3,190}$ = 1.48, p = 0.22) and year ($F_{2,190}$ = 2.81, p = 0.06) increased. Nonetheless, within all reservoirs, ovary size during autumn varied between years.

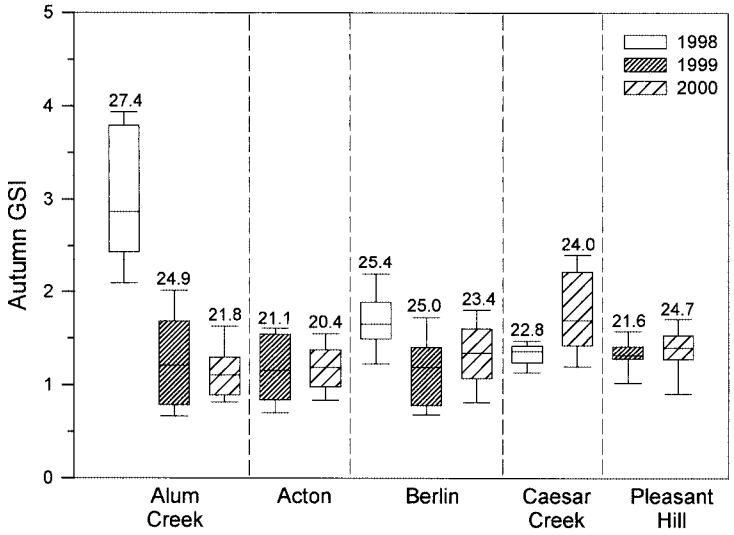

Fig. 2. Autumn gonadosomatic index (GSI) of white crappie collected between the second week in October and the first week in November, 1998–2000, from five Ohio reservoirs. Horizontal lines inside the box represent the median GSI, box ends represent the 25th and 75th percentiles, and error bars represent the 10th and 90th percentiles. Numbers above the error bars represent mean fish length (cm) sampled. Vertical dashed lines separate reservoirs.

Dynamic programming results

Optimal allocation of energy to somatic growth, κ, was much more sensitive to spring than summer feeding conditions. To illustrate this general result, we focus on 3-year-old fish. All fish larger than 20 cm initiated allocation to reproduction during autumn, and predicted allocation was dependent on feeding conditions in the coming spring. Across all possible treatments of summer and spring feeding conditions (i.e. both constant and variable spring feeding conditions), optimal autumn allocation varied among fish of similar lengths (see Fig. 3), especially for small fishes. Small differences among expected fitness values (e.g. < 0.2%) for the highest and second or third highest associated allocation values caused this variability in optimal allocation. Despite this variability, general trends were apparent for all treatments. When spring feeding conditions were always good, small white crappie allocated nearly all of their energy to somatic growth during autumn, whereas larger fish allocated up to 70% of resources to ovary development (Fig. 3a,b). Size of ovary coming into autumn had a predictable effect: those fish without ovary mass allocated more energy to ovaries than those with about 25% of their maximum ovary mass already achieved. In addition, recent good summer feeding conditions (Fig. 3b) did not increase energy allocation to ovaries during autumn, compared to recent poor

summer feeding conditions (Fig. 3a). When spring feeding conditions were always poor (Fig. 3c,d), all sizes of white crappie allocated more energy to ovaries during autumn than when spring feeding conditions were always good (compare Figs 3c,d and Figs 3a,b). Again, summer feeding conditions had no observeable impact on optimal allocation, and fish entering autumn

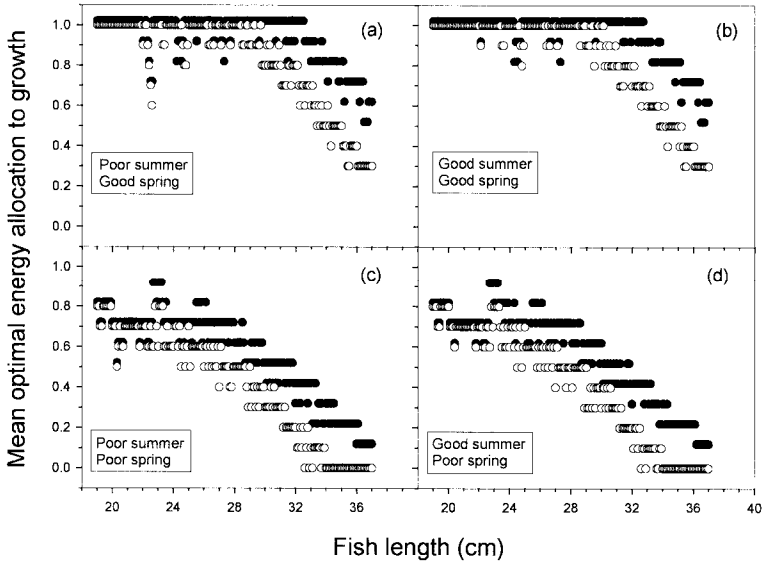

Fig. 3. Optimal proportion of energy allocated to somatic growth (κ) during autumn by a simulated 3-year-old white crappie as a function of fish length, when quality of summer and spring feeding conditions is constant across years. Quality of spring and summer feeding conditions is indicated as poor (P_1 = 0.2, ρ_1 = 1.0) or good (P_1 = 0.6, ρ_1 = 1.0). Ovary mass at the beginning of autumn was 0 g (○) or 25% of maximum ovary mass (●). Data illustrated with solid circles were offset by 0.02 to allow all points to be seen.

with larger ovaries allocated less energy to reproduction than those entering autumn with smaller ovaries.

The probability of poor spring feeding conditions had a strong influence on optimal autumn allocation to ovaries. Across four probabilities of poor spring feeding conditions, we compared the mean optimal allocation of six different centimetre size classes of white crappies to demonstrate this effect. When the probability of poor spring feeding conditions was only 1% (corresponding to a 99% probability that spring feeding conditions are good), the allocation pattern did not differ considerably from a system in which poor spring feeding conditions never occurred (Fig. 4a,b). However, when the probability of poor spring feeding conditions increased from 1% to just 10%, then the allocation pattern closely resembled when poor spring feeding conditions occurred every year (Fig. 4a,b). Thus, only a small probability of poor spring feeding conditions initiated a considerable proportion of energy allocated to ovaries. These size classes demonstrate the general effect of size: optimal allocation of energy to ovaries increased with fish

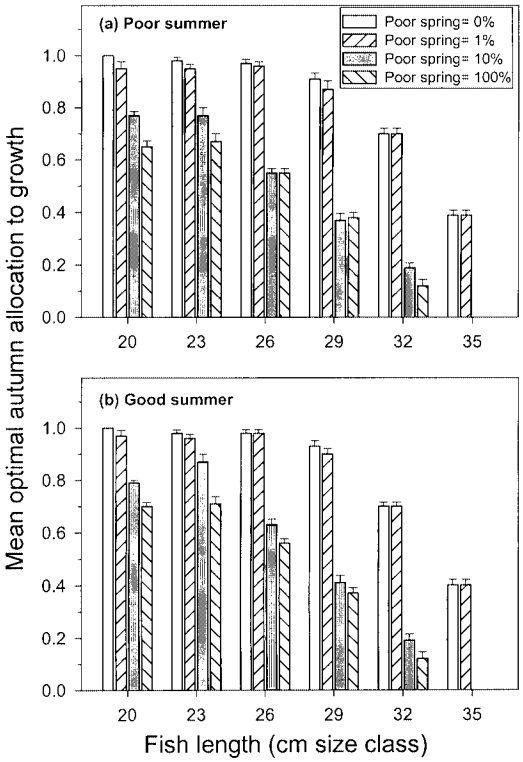

Fig. 4. Mean (± standard error) autumn optimal allocation to somatic growth (κ) of a 3-year-old white crappie as a function of fish length. Poor spring feeding conditions (*P1* = 0.2) occurred with probability ρ_1 = 0.0, 0.01, 0.10 or 1.0; good spring feeding conditions *(P_2=0.6)* occurred with probability ρ_2=1- ρ_1. Summer feeding conditions were either (a) poor (P_1 = *0.2*) or (b) good (P_1 = 0.6) with probability ρ_1 = *1.0.* For both panels, mean allocation was calculated across a centimetre length class (i.e. across ten 1 mm size classes). The mean optimal allocation to somatic growth for fish measuring 35 cm in length was 0 when poor spring feeding conditions were predicted to occur in 10 and 100% of years.

size across all treatments. Similar to the results when spring feeding conditions were constant, summer feeding conditions did not influence optimal allocation, and fish entering autumn without ovary mass allocated more energy to reproduction than those entering autumn with ovaries that were 25% of maximum mass.

Again focusing on 3-year-old fish, we looked at allocation to reproduction during summer. During summer, nearly all energy was allocated to somatic growth. In fact, energy was never allocated to reproduction during summer for fish less than 32 cm in length. Larger fish allocated between 10 and 30% of energy to reproduction, depending on the probability of poor feeding conditions during spring, at least 9 months later. In model runs in which good spring feeding conditions occurred in at least 99% of years, only fish longer than 36 cm allocated energy to reproduction in summer (and that proportion was 0.1). When poor spring feeding conditions occurred in at least 10% of years, fish longer than 32 cm allocated up to 30% of energy to reproduction. Percent allocation to reproduction increased with fish length and decreased with increasing mass of ovary entering the summer. Summer feeding conditions did not have a direct influence on allocation patterns. Thus, summer allocation to reproduction occurred only for large fish.

Individual-based model results

We present results only from autumn, as allocation to reproduction occurred at nearly all sizes of fish and we could compare ovary growth of modelled fish to that of fish sampled in the field during autumn. First, to ensure that our model grew white crappie at reasonable rates, we compared the growth rates of modelled fish at various feeding conditions to those captured in Ohio reservoirs. Mean length at age of modelled fish overlapped considerably with mean length at age of field fish, especially for 3-year-old fishes (Fig. 5). Hence, the seasonal feeding conditions used in our models appear to set reasonable estimates of consumption. We also calculated the GSI at the end of the spring (just before spawning) to determine whether modelled fish maximized ovary size. When summer and spring feeding conditions were constant, all simulated fish attained the maximum ovary size possible. When spring feeding conditions were uncertain, all fish still nearly attained their maximum ovary size (i.e. greater than 96% of maximum).

When summer and spring feeding conditions were constant across years, autumn GSI was driven by spring feeding conditions (Fig. 6). Because ovary size increased with fish size, we first used only fish less than or equal to 28 cm in length to ensure common size comparisons when comparing across treatments of different feeding conditions. In this case, the mean autumn GSI was always less than 1.0 when spring feeding conditions were relatively good (i.e. when $P_1 > 0.3$, $\rho_1 = 1.0$; Fig. 6a). Mean autumn GSI exceeded 1.0 only when spring feeding conditions were poor (i.e. when $P_1 \leq 0.3$, $\rho_1 = 1.0$; Fig. 6a). When mean autumn GSI was calculated using fish of all lengths (Fig. 6b), the general pattern of decreasing mean autumn GSI with improving spring feeding conditions remained. However, both mean GSI and standard errors were higher when all sizes were included, because ovary size and GSI increased with fish size. When comparing the effects of summer feeding conditions, mean autumn GSI differed little between good and poor summer feeding conditions at similar fish lengths (Fig. 6a); however, across all fish lengths, good summer feeding conditions produced larger fish than poor summer feeding conditions. With the inclusion of larger fish, mean autumn GSI increased (Fig. 6b), because of the higher GSI associated with larger fish.

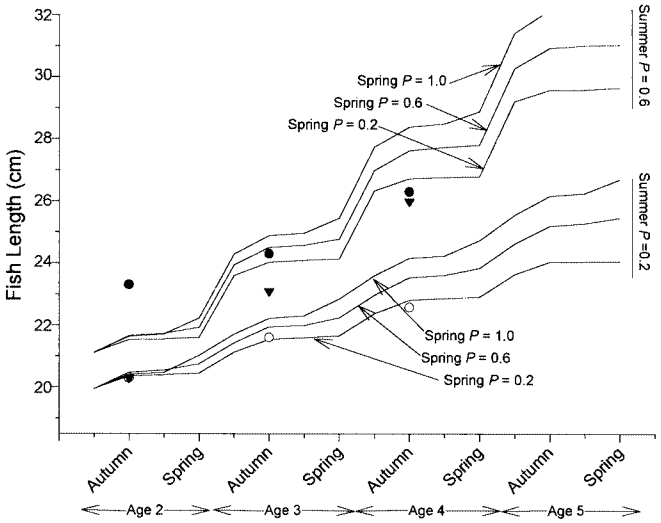

Fig. 5. Growth trajectories of white crappie, including both modelled fish that experience different summer and spring feeding conditions and fish collected from three Ohio reservoirs (●, Caesar Creek; ○, Acton; ▼, Pleasant Hill), as a function of age and season. Modelled fish lengths are depicted by solid lines. Symbols indicate mean

length (cm) of fish sampled from three reservoirs for the 1996 year-class, during autumn 1998 (age 2 years), 1999 (age 3 years) and 2000 (age 4 years) (D.B. Bunnell, unpublished data).

To explore how uncertainty in spring feeding conditions influenced somatic and reproductive growth, we varied the probability of poor spring feeding conditions. When poor spring feeding conditions occurred in at least 10% of years, mean GSI was at least 1.4 when using fish of similar sizes (Fig. 7a) and at least 2.0 when all sizes of fish were included (Fig. 7b). Only when the probability of poor spring feeding conditions was less than 5% was the mean GSI less than 1.0. Thus, mean GSI was remarkably similar when poor spring feeding conditions always occurred and when they occurred in only 10% of years (i.e. a 90% probability that spring feeding conditions will be good). The inclusion of larger fish, either through good summer feeding conditions or by including all sizes of fish in calculating the mean (Fig. 7b), increased autumn GSI.

DISCUSSION

For spring-spawning fish that grow somatically after maturity, our model described the optimal time to begin allocating energy to reproduction following a reproductive event, given the trade-off between current reproductive development and somatic growth towards future reproductive development, under different summer and spring feeding conditions. We focused on autumn because many spring-spawning fish begin energy allocation to reproduction during this season (Adams *et al.*, 1982a; Henderson and Nepszy, 1994; Henderson *et al.*, 2000), which, in turn, reduces the length and commensurate fecundity that could have been attained by spring. In addition, the results of our model showed that considerable allocation to reproduction occurs during autumn for nearly all sizes of fish (i.e. fish greater than 20 cm in length). Only very large

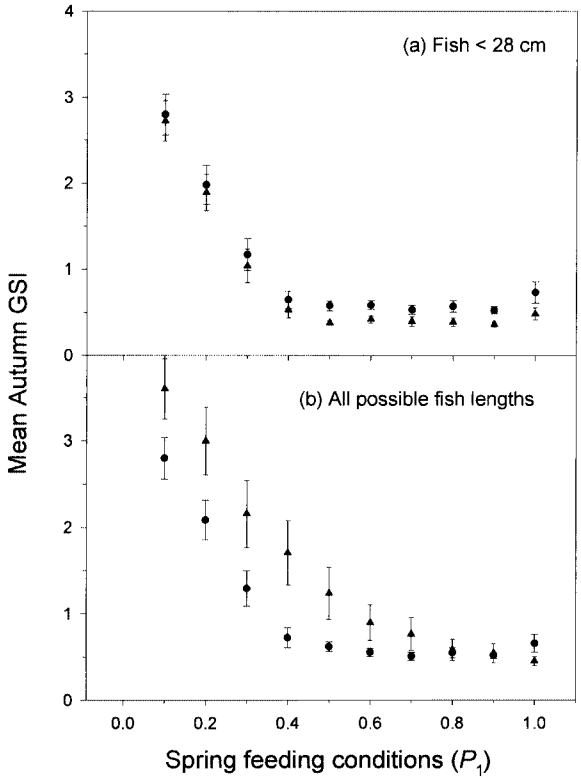

Fig. 6. Mean autumn GSI (± standard error) of modelled white crappie as a function of constant spring feeding

conditions, P_1 (where $\rho_1 = 1.0$). For each panel, summer feeding conditions are either poor ($P_1 = 0.2$, $\rho_1 = 1.0$; ●) or good ($P_1 = 0.6$, $p_1 = 1.0$; ▲). (a) Fish less than 28 cm in length, which represents the largest common length for all summer and spring feeding conditions. (b) Fish from all length classes in which greater than 50% of the simulations contained fish in that length class.

fish (i.e. length > 32 cm) allocated energy to reproduction during summer, and then only a small amount. We used the model to evaluate whether early allocation to reproduction was a plastic response to recent good feeding conditions during summer or an evolutionary response to the poor feeding conditions in the coming reproductive season. The possibility of poor spring feeding conditions regulated autumn allocation to reproduction; summer feeding conditions had no direct impact. The autumn GSI of modelled white crappies making optimal decisions matched that of white crappies sampled from Ohio reservoirs when modelled white crappies were faced with at least a 10% probability of poor spring feeding conditions. When spring feeding conditions were always good or when poor spring feeding conditions occurred with a probability of less than or equal to 5%, the GSI of 'modelled' white crappies was less than that of white crappies sampled from Ohio reservoirs. In our view, the risk that the coming spring may not provide enough food to build ovaries to their maximum size has selected for white crappies to begin allocating energy to ovaries, in addition to somatic growth, during autumn.

In our model, white crappies were permitted to allocate energy only to somatic growth or ovaries; allocation to energy storage was not permitted. Although white crappies do

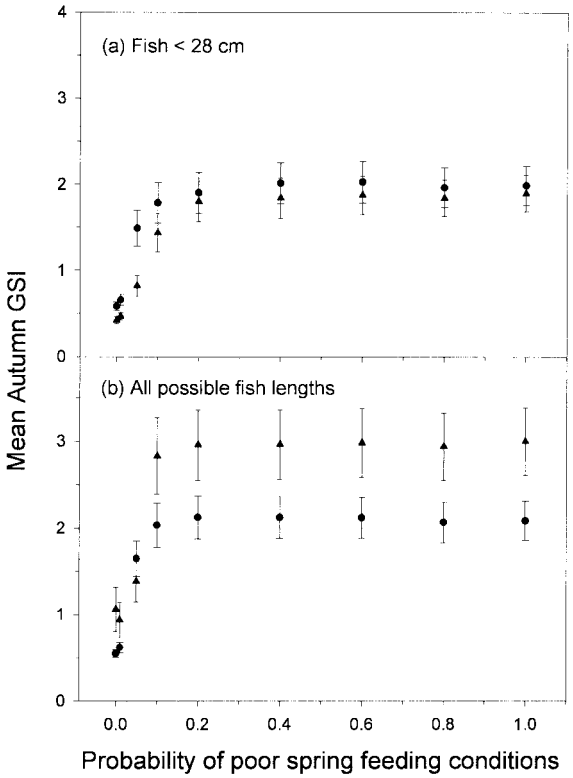

Fig. 7. Mean autumn GSI (± standard error) of modelled white crappie as a function of the probability, p_1, that poor spring feeding conditions ($P_1 = 0.2$) occurred. The alternative to poor spring feeding conditions was good spring feeding conditions ($P_2 = 0.6$). For each panel, summer feeding conditions are either poor ($P_1 = 0.2$, $\rho_1 = 1.0$; ●) or good ($P_1 = 0.6$, $\rho_1 = 1.0$; ▲) every year. (a) Fish less than 28 cm in length, which represents the largest common length for all summer and spring feeding conditions. (b) Fish from all length classes in which greater than 50% of the simulations contained fish in that length class.

accumulate visceral lipid stores, our model assumed that gonads are developed directly from prey resources, a strategy referred to as 'income' breeding (Stearns, 1992). Other organisms, including some fish, frogs, lizards and birds (Henderson and Nepszy, 1994; Chastel *et al,* 1995; Doughty and Shine, 1998; Bonnet *et al,* 2001), are 'capital' breeders in that they rely more upon energy stores than on incoming food to fuel development of reproductive tissue (Stearns, 1992). Although the reproductive strategy of white crappie is unknown, we assume white crappie to be 'income' breeders (i.e. permitting allocation only to somatic growth or ovaries) in this model. From a reproductive perspective, storage of energy in ovaries is somewhat analogous to storage of energy in visceral fats, except that energetic losses associated with converting stored energy to gonadal tissue are omitted (Jönsson, 1997; but see Bonnet *et al*, 1998). Thus, relative to a model in which fish were permitted to store energy viscerally, our model may be biased towards more allocation to ovaries in autumn. Energy stores may also be important in supplementing energetic needs during times of low food availability, such as in winter. In our model, only energy available for growth – that is, after basic energetic maintenance needs have been met – could be allocated to somatic growth or reproduction. Despite not including energy storage, our model still expresses the basic trade-off between immediate reproductive development (allocating to gonads or energy stores) and somatic growth towards future reproductive development (allocating to somatic growth).

Is autumn energy allocation a plastic response to summer feeding conditions?

Phenotypic plasticity in energy allocation suggests that energy allocation decisions can respond to changes in the environment (e.g. changes in food amount). Experimental work has revealed that organisms can either increase or decrease reproductive allocation in response to significant changes in feeding conditions (e.g. Aronson *et al.,* 1992; Cheung and Lam, 1999; Stelzer, 2001). In building this model, we hypothesized that allocation to ovaries during autumn would be high following summers with good feeding conditions. Specifically, we thought white crappie might capitalize on abundant summer prey by beginning ovary development during autumn in preparation for reproduction 6-7 months later.

Inter-annual variability in early ovary development can be explained by a plastic response to recent (summer) feeding conditions. For the field data, we were able to assess autumn energy allocation through ovary mass. Here, we found support for plasticity in energy allocation decisions: there was a significant interaction between reservoir and year, indicating that ovary size (using residual ovary mass as an index) differed across years within a reservoir. The model results, however, suggested that summer feeding conditions do not have a direct influence on optimal energy allocation. Dynamic programming revealed that autumn allocation of energy to ovaries for a fish of a given size was not higher following summers of good feeding than following summers of poor feeding. Similarly, optimal allocation during summer was not influenced by summer feeding conditions. Summer feeding conditions, however, will have a considerable impact on fish size. Because fish size influences energy allocation in all combinations of summer and spring feeding conditions, summer feeding conditions will have an indirect influence on energy allocation through its effect on fish size.

Initial support for the hypothesis that early energy allocation to ovaries would follow summers of good feeding conditions derived largely from observations of capital breeding organisms. For many of these taxa, the months preceding commencement of gonadal development influence later reproductive output. For example, summer feeding is critical to

determining the percent of mature walleye that ultimately will spawn the following spring (Henderson and Nepszy, 1994; Henderson *et al,* 1996). Excellent summer feeding leads to high energy stores, upon which walleye rely to fuel reproductive development (Henderson *et al,* 1996). Prey resources during seasons well before reproduction have been shown to influence the reproductive output of other taxa, including female aspic vipers (*Vipera aspis:* Bonnet *et al,* 2001), southern water skink (*Eulamprus tympanum:* Doughty and Shine, 1998) and guppies (*Poecilia reticulata:* Reznick and Yang, 1993). However, good feeding conditions during pre-reproductive seasons for 'capital' breeding taxa do not necessarily have a direct influence on energy allocation to reproduction, but rather have a greater impact on energy stores. These higher energy stores, in turn, influence energy allocation decisions about reproduction. Thus, for both modelled white crappie and some capital-breeding taxa, success of feeding in seasons before the start of reproductive allocation has a direct influence on the state (e.g. length, energy stores) of an organism, which, in turn, may later influence energy allocation decisions regarding gonadal tissue.

Is autumn energy allocation an evolutionary response to spring feeding conditions?

Our second hypothesis was that feeding conditions during spring, the season leading to reproduction, would influence allocation decisions in the previous autumn. Of course, white crappie cannot predict feeding conditions 6 months in the future. Thus, if modelled white crappie are responding to probabilities of future spring feeding conditions, then this can be viewed as an evolutionary adaptation to an environment. In our model, the probability of poor spring feeding conditions influenced optimal allocation to ovaries during the preceding autumn. First, when poor spring feeding conditions always occurred, some allocation to ovaries during autumn was generally optimal. The more surprising result was that a similar allocation to ovaries was observed when poor spring feeding conditions had only a 10% probability of occurring. Thus, the model results suggest that the consistent autumn allocation to ovaries observed in white crappie in Ohio reservoirs is a response to the possibility of poor feeding conditions in the coming spring.

In addition to matching our field data, the model results match energy allocation field data from fish sympatric with white crappie. In general, those fish reproducing before or at the same time as white crappie also begin allocating energy to ovaries during autumn. Conversely, those fish reproducing later in summer wait until spring or early summer to begin allocating energy to ovaries, when good feeding conditions will occur with a higher probability. Walleye (Henderson and Nepszy, 1994), yellow perch (Henderson *et al.*, 2000), northern pike (*Esox lucius*: Diana and Mackay, 1979) and largemouth bass (Adams *et al.*, 1982a) all reproduce during early or late spring (Amundrud *et al.*, 1974; Auer, 1982), before or during white crappie reproduction, and begin building ovary mass during autumn. Conversely, bluegill *Lepomis macrochirus* reproduce later in summer and wait until late spring or early summer to initiate ovary development (Morgan, 1951). It would be interesting to document autumn energy allocation patterns of white crappie in the more southern extent of their range. If feeding conditions are improved either during winter and spring in the southeastern United States, relative to Ohio, then more southerly populations may wait until spring to begin allocating energy to ovaries.

Spring feeding conditions in Ohio can be uncertain for several reasons. First, consumption in poikilotherms is a function of temperature (Jobling, 1994) and spring temperatures are quite variable across years. Second, gizzard shad *Dorosoma cepedianum*, the primary prey of

adult white crappie in Ohio reservoirs, are susceptible to high mortality during long cold winters (Adams *et al.*, 1982b); thus, variability in winter severity causes variability in potential spring feeding conditions. Finally, white crappie population densities are quite variable between years (McDonough and Buchanan, 1991). If intraspecific competition affects feeding conditions, variable population densities can lead to variable success in spring feeding.

Uncertainty in future feeding conditions (i.e. prey availability, length of growing season) results in theoretical predictions of simultaneous or 'intermediate' allocation of energy to growth and reproduction. In previous models, this pattern provided evidence for optimality of somatic growth after maturity (e.g. King and Roughgarden, 1982; Gurney and Middleton, 1996; Kozlowski and Teriokhin, 1999). In our model, in which somatic growth after maturity was expected, the timing of this 'intermediate' allocation was our focus.

As the probability of poor feeding conditions in spring exceeded 10%, earlier allocation to reproduction became optimal. Thus, even a small probability of an unfavourable spring resulted in a 'bet-hedging' strategy where somatic growth and future fecundity were compromised in favour of early reproductive development in autumn. Analogous to previous models (e.g. King and Roughgarden, 1982), a 'bang-bang' strategy of 100% energy allocation to somatic growth followed by a switch to 100% allocation of energy to reproduction was no longer optimal when uncertainty in future feeding conditions was introduced.

Summary

For white crappie or other organisms that grow after maturity and whose fecundity is related to body size, a trade-off exists between reproductive events: begin immediate reproductive development or grow to enhance future potential fecundity. Dynamic programming models revealed initiation of reproductive development to be regulated by future probabilities of poor spring feeding conditions rather than recent summer feeding conditions. When 'modelled' white crappie were faced with at least a 10% probability of poor spring feeding conditions, their autumn reproductive investment (gonadosomatic index) was similar to that of fish collected from Ohio reservoirs. Thus, uncertainty about future feeding conditions, which predicts growth after maturity in previous models, also predicts that energy allocation to reproduction will begin early, at the expense of continued somatic growth that could increase later potential fecundity.

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